LARVAE OF ALBERTA TANYDERIDAE (DIPTERA: NEMATOCERA)

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Tanyderid larvae, probably of Protanyderus, *have been found in the middle reaches of the Old Man, Sheep, Red Deer, Athabasca and Cutbank Rivers of Alberta.*

The usual habitat, in shallow, fast flowing water, is of sand and gravel through which the larvae burrow.

Live larvae were kept in the laboratory and observations show that they move over surfaces by pulling the body forward with the head and pushing with the posterior pseudopods. Burrowing involves the head, but also waves of contraction passing forward along the body. The filamentous tracheal gills are sometimes held above the substrate.

The external structures of representative larvae are described and figured with SEM micrographs. Older larvae are amphipneustic, but probable second instar larvae are metapneustic with apparently non functional spiracles.

Larvae are well adapted for burrowing. Head and mouthparts are heavily sclerotized, and are scratched and worn; spiracles are flush or below the body wall, which itself is tough and microsculptured; and the filamentous, terminal gills and the pseudopods can be held together.

Gut and fecal pellet contents show only plant material similar to that in the habitat.

No adult or pupal tanyderids are yet known from Alberta.

Nous avons découvert en Alberta les larves appartenant probablement au genre Protanyderus *le long des rivières suivantes à mi-chemin de leur source: Old Man, Sheep, Red Deer, Athabasca, et Cutbank.*

L'habitat normal est en eau peu profonde et rapide. Le lit consiste de sable et de gravelle dans lequel les larves creusent.

Nous avons gardé en captivité des larves pour observations. Nous avons noté qu'elles se déplacent en tirant le corps vers l'avant avec la tête et en poussant avec les pseudopodes postérieurs. La tête et des contraction ondulées vers l'avant le long du corps participent au creusage. Les ouies trachéales et filamenteuses demeurent quelquefois au-dessus du sol.

Nous avons décrit et illustre à l'aide du microscope à balayage electronique les structures externes de larves représentatives. Les larves plus agées sont amphipneustiques, alors que probablement des larves au deuxième stade sont metapneustiques et apparemment sans stigmates fonctionnelles.

Les larves sont bien adaptées pour creuser. La tête et les parties mandibulaires sont fortement sclérosées, égratignées et usées; Les stigmates sont à la surface ou légèrement sous la surface du corps qui elle-même est dure et microsculpturée; et les ouies filamenteuses et terminales demeurent ensembles.

Le contenu de l'intestin et les boules fécales ne montrent que des matière végétaux semblables à celles trouvees dans leur habitat.

Nous ne connaissons pas encore la pupe et l'adulte des Tanyderides de l'Alberta.

The Tanyderidae or Primitive Crane Flies are a cosmopolitan Family of 11 genera and some 36 species. Four genera with 18 species are concentrated in Australasia with only two genera and four species known from North America (Alexander and Alexander 1967, Colless and

McAlpine 1970). Osten Sacken (1859) included tanyderids in the Tipulidae, but they were placed in the Ptychopteridae by Handlirsch (1909) and others, until Alexander (1919) on the basis of wing venation, raised the group to familial status (Williams 1933).

Alexander (1930) reported large swarms of adult *Protoplasa fitchii* (Osten Sacken) occurring in Quebec, nevertheless tanyderids are considered to be amongst the rarest of all Diptera (Alexander and Alexander 1967).

Because of the adult wing venation, Tanyderidae are considered to be the most primitive of the nematocerous Diptera (Crampton 1930, Alexander 1930, Williams 1933, Imms 1957, Oldroyd 1964, Colless and McAlpine 1970 and Hennig 1973). As the larvae might be of considerable phylogenetic importance both Crampton and Alexander expended considerable effort to find larval Tanyderidae. Crampton (1930) describes their efforts in a fascinating paper, recalling the backbreaking work to find the larvae, and their surprise at seeing that the larvae were not like they had expected. The larvae are eucephalous, amphipneustic, with six spectacular terminal tracheal gills, four anal papillae and two ambulatory pseudopods with hooks (Fig. 1).

No other tanyderid larvae were discovered until Wood (1952) found those of the African *Peringueyomyina barnardi* Alexander in 1937. These larvae have only short, stumpy terminal gills.

Rose (1963) assigned one Californian larva to *Protanyderus vipio* (Osten Sacken). Knight (1963, 1964) described, respectively, the supposed larva and pupa of *P. margarita* Alexander from Colorado. Colless and McAlpine (1970) figured the larva of the Australian *Eutanyderus wilsoni* Alexander, and Hinton (1966) described the pupal gill derived from that material which was originally collected in 1964 and 1965 (Colless, *in litt.* 1975). One large larva, probably of *Protanyderus,* was collected in 1957 from the same stream as was the larval *P. vipio* and deposited in the U.S. National Museum, but not reported (P.D. Hurd, *in litt.* 1975). Two other tanyderid larvae from the Cache la Poudre River, Colorado, 1973 are known (H.E. Evans, pers. comm. and *in litt.* 1975).

Apart from the *Protoplasa fitchii* material from Quebec, there appears to be only one other record of Canadian Tanyderidae, a single adult of *P. margarita* from Seton Lake, British Columbia, collector J. McDunnough, 1933 (Canadian National Collection. G. Shewell, *in litt.* 1974).

It was exciting therefore when five larval tanyderids were collected in Alberta by R.C.B. Hartland-Rowe, Department of Biology, University of Calgary, from the Sheep River, Turner Valley, in 1972, and two larvae were collected from the Cutbank River, Alberta, by F. Bishop, Regional Fishery Biologist, Alberta Department of Recreation, Parks and Wildlife, Peace River, in 1973. In 1974 a series of tanyderid larvae from the Old Man and Red Deer Rivers became available *via* K. Exner, Department of Environment, from a Macrobenthic Fauna Survey of Alberta Rivers (Reynoldson 1974, Briggs 1975). K. Depner, Canada Agriculture, Lethbridge recovered tanyderid larvae from the Athabasca River during the Athabasca Blackfly Research Program in 1974. Details of the above sites are given below.

As no pupae or adults have yet been associated with the Alberta larvae, the taxonomic position of this material is not clear. Map 1 shows that *Protoplasa* is restricted to northeastern North America and *Protanyderus* to the west. However, unlike the larvae and pupae of *Protoplasa fitchii* which were associated by rearing to adults of that species (Alexander 1930, Crampton 1930), the supposed immatures of *Protanyderus vipio* and *P. margarita* were not thus associated (Rose 1963, Knight 1963, 1964), and morphological discrimination of larvae of the two genera is difficult at present because of paucity of material. But *Protoplasa* larvae lack the sclerotized knob above the antenna which is variously developed in the supposed larvae of *Protanyderus* and in the Alberta material, and larval *Protoplasa* have fewer pseudopod hooks than the other larvae.

As Alberta larvae are morphologically more similar to the supposed larvae of *Protanyderus* than to those of *Protoplasa*, and since only *Protanyderus* is known from the West, the Alberta larvae are probably of *Protanyderus*. The distribution of *Protanyderus margarita* (Map 1) further suggests that the Alberta larvae may be of that species.

The discovery of tanyderid larvae in larger rivers is surprising, for, with the exception of larval *Eutanyderus wilsoni* which inhabit the surface of rotten logs in cold streams (Colless, *in litt.* 1975), the other tanyderid larvae have been found in smaller gravely streams. Therefore, a rather detailed description of the Red Deer River habitat (Fig. 2, 3) is given so that biologists working in similar habitats may be alerted to the possibility of tanyderid larvae occurring there.

Detailed descriptions of the external form and structure of the Alberta tanyderid larvae are given here to provide a basis for comparison with larvae of other tanyderid genera. Description of the internal structure of the larvae is in progress and will be used in a detailed comparative account on tanyderid larvae to be published later elsewhere.

MATERIAL AND METHODS

Material was obtained from the following Alberta localities (Map 1):

Old Man River. (Collector, Department of Environment). – Fort MacLeod Bridge, Highway #2. 16 April, 1974; 21 April, 1975. Monarch Bridge, Highway #3. 23 October, 1974.

Sheep River, Turner Valley. (Collector, Hartland-Rowe). – Western Decalta, Turner Valley Gas Treatment Plant. 25 October; 14 November, 1972.

Red Deer River. (Collectors, Department of Environment and/or Craig). – Raven River (2.4 km upstream of confluence). 12 June, 7 August, 17 September, 1974; 19 July, 12 August, 1975. Raven River Confluence. 12 June, 1974, 7 August, 1975. Innisfail Bridge (0.94 km downstream). 14 May, 17 May, 10 July, 18 October, 1974; 16 May, 25 May, 12 June, 9 August, 11 August, 1975. Dickson Camp Site, 13 June, 1974; 9 July, 11 August, 1975. Dickson Camp Site (3.4 km downstream). 23 June, 1974. Dickson Camp Site (11.0 km downstream) 24 June, 1974; 12 August, 1975. Dickson Camp Site (15.2 km downstream). 12 August, 1975.

Athabasca River, (Collector, Depner). – 19 km upstream Athabasca Township, 28 May, 1974. 90 km upstream Athabasca Township, 11 July, 1974.

Cutbank River (Collector, Bishop). – 23 May, 1973.

Two main collecting techniques were successful. Exner used a stainless steel cylinder with a cross sectional area of 0.093 square meters (1 sq. ft.). This was pushed into the substrate and the entrapped material disturbed to a depth of about 15 centimeters. The dislodged material was caught in a 210 μm net attached on the downstream side of the cylinder (Reynoldson, 1974). Craig used 0.7 mm mesh drift nets and disturbed the substrate upstream of the nets for a few meters with a spade. Samples were made in swift, shallow water to a maximum depth of 45 cm. From a standard five samples usually only one or two larvae were recovered. Once four larvae were recovered from a single sample with a drift-net. Large numbers of many other aquatic insects were recovered in the samples. Other collectors disturbed the substrate and caught dislodged material with a long-handled dip net.

Some material was fixed in isopropyl alcohol, and in alcholic Bouins fixative. Normal techniques were used for light microscopy. Three larvae were examined using SEM techniques described by Craig (1974). Figures 16 and 25-36; Figures 8, 17, 18 and 37-39; and Figures 4-7, 9-15 and 19-24 are of specimens from the Cutbank River, and the Dickson and Innisfail sites, Red Deer River, respectively.

Live material kept well in a Petri dish with a small amount of sand, gravel and detritus at 6 C. Specimens also survived at room temperature (20 C), one for 12 months, in vials with two inches of sand and gravel with water. None have grown larger.

Where applicable the terms of Knight and Laffoon 1973, Anthon 1943 and Hennig 1973 are used.

A permament record of larval behaviour was made with a Super-8 cine camera.

HABITAT

The Red Deer River is a major Alberta stream (mean discharge at Red Deer 51.25 m^3/sec.), with headwaters in the Rocky Mountains northeast of Lake Louise, Banff National Park.

At the city of Red Deer the river is ice-covered for approximately 158 days of the year (mean freeze-up Nov. 6; mean break-up April 13). It is 20-30 m wide during the summer, with a maximum depth of 1.5 m. The river valley is stream cut and forested with white spruce and aspen poplar. Willow thickets intervene in floodplain areas. The channel pattern is one of irregular meanders with a pool and riffle sequence, and occasional diagonal and mid-channel bars. Bed material is predominantly gravel. Sieve analysis shows that 90% of the bed material is finer than 95 mm, 65% is finer than 60 mm and 50% is finer than 48 mm. (Kellerhals 1972).

The Innisfail site (Fig. 2), where the largest collections of larvae were made (32.6 km upstream of Red Deer), is characterized by an extensive gravel floodplain along the left bank. Sampling equipment was easily set in the loosely packed gravel bed (Fig. 3). Although the depth of the gravel below the streambed is not known, pit-digging a few meters from the water line showed the gravel to be well saturated, with occasional Chironomidae larvae and Plecoptera nymphs observed. The area possibly supports an extensive hyporheic community of invertebrates, that is organisms living in the interstices of the bed material (Schwoerbel 1967). The stream bed has much detrital material, most of which is woody and probably originates from abrasion of drifting trees and bush during high water levels, while the remainder is likely leaf litter and other windblown material.

The pH of the river near the main collecting site is 7.8-8.2 (mean 8.0), total alkalinity 190-250 mg/1, $CaCO_3$ and hardness values as $CaCO_3$ 200-250 mg/1, total dissolved solids 220-280 mg/1, specific conductance 420-500 umho/cm, average total phosphorous and nitrogen concentrations less than 0.025 mg/1 and 0.4 mg/1 respectively, mean dissolved oxygen concentrations from December to March approximately 9.5 mg/1 (Briggs 1975).

The Old Man River at Fort MacLeod has a shorter ice cover period (approximately 125 days), and a lower flow rate (mean discharge 38.23 m^3/sec.) than the Red Deer River. The bed is not as rich in detritus as that of the Red Deer River, reflecting the shrub and grass covered valley walls. The similarity between the two sites is in the bed material. The Old Man River channel bed is predominantly gravel (90% finer than 101 mm,65% finer than 0.1 mm, and 50% finer than 49 mm) which is loosely packed (Kellerhals 1972). The reach near Fort MacLeod is also associated with a prominent and frequently flooded valley flat. Water chemistry above Lethbridge is similar to that at Innisfail. Ranges for the following parameters are: pH 8-8.3, total alkalinity 145-160 mg/1, hardness expressed as $CaCO_3$ 175-250 mg/1, total nitrogen, less than 0.2 mg/1, total phosphorous, less than 0.1/mg/1, conductivity 240-325 umho/cm, dissolved oxygen 10.8-13.7 mg/1 (Konopasek 1972).

The Cutbank River site (Bishop, F. 1973) shows some similarities to the Red Deer and Old Man sites. The river is smaller, but has forested banks and a substrate mainly of boulders and sand-silt. Water chemistry analyses show the following values: pH 8.1, total alkalinity 120-239 mg/1, total dissolved solids 90-165 mg/1, nitrate nitrogen 3.0-9.0 mg/1, total phosphate 0.02-0.03 mg/1, and dissolved oxygen 14-15 mg/1.

Other isolated collections of tanyderid larvae have been made in habitats somewhat different from those described above. The five larvae from the Sheep River, Turner Valley were taken from a fine sand-mud substrate in the vicinity of the effluent of a natural gas treatment plant.

Larvae from the Athabasca River came from a substrate of loose rock and gravel with the temperatures 11.5 and 16 C respectively and high water velocity.

MORPHOLOGY: EXTERNAL FEATURES

Larval Instars

A preliminary analysis of larval head-width frequency distribution, number of pseudopod hooks and presence or absence of spiracles indicates only two larval instars in the Alberta material. One larva very much smaller than any other was collected, but unfortunately was lost before examination.

As most nematocerans have four larval instars (Hennig 1948, Craig 1975), and because of the single small larva seen and the two other distinct size classes of larvae, we believe that the material we have represents second and third instar larvae.

Early Instar (2nd?)

Three specimens. Head-width, 0.36 - 0.38 mm, metathoracic width, 0.64 - 0.80 mm, depth, 0.32 - 0.76 mm; total body length (from behind head to tip of tracheal gill), 10.0 - 11.2 mm; gill length (from posterior spiracle), 2.40 - 3.34 mm.

Generally similar to later instar larvae, but is metapneustic (sections show no trace of the prothoracic spiracles and the posterior abdominal spiracles to be non-functional). Pseudopods with 14 distal hooks and five basal hooks.

Later Instar (3rd?)

Head capsule. Greatest width $\overline{X} = 0.60 \pm 0.05$ mm; N = 28. Eucephalous, essentially prognathous (Fig. 4). Massively sclerotized and heavily pigmented anteriorly (Fig. 5). Posterior head region retracted into prothorax. Posterior arm of ecdysial suture (Ecs.) at least one third (Fig. 21) length head (light microscopy shows this suture to be deeply invaginated, externally evidenced in Fig. 24). Lateral arms of ecdysial suture divergent at sharp angle toward antennae, but convergent anteriorly before antennal level and in contact with pits on epistomal ridge (Epr.) (Fig. 22). Epistomal ridge (Epr.) massive, with four anteriorly projecting lobes above membranous labrum (Fig. 5, 9, 22).

Antennae anterolaterally immediately caudad of mandible. Antennal sclerite heavily sclerotized and raised caudad and dorsad of antenna (Fig. 4). Two articles, basal one ring-like and only sclerotized posteriorly. Second article twice as long as wide, with campaniform sensillum (Cmp.) distally (Fig. 7). Large cone shaped apical sensillum (Aps.) with pores, at least eight smaller sensilla at its base (Fig. 8). Antenna inserted beneath large sclerotized knob (Fig. 21, 23).

Mandibles massive, pyramidal in shape (Fig. 17). Four apical teeth form narrow spoon-like region (Fig. 18). Median tooth projects well beyond other teeth, ventral teeth with low profile. Proximal to scoop-like region a slight raised area ("hakenformiger Versprung" (?) of larval Tipulomorpha and Psychodomorpha, Anthon 1943).

Dorsal articulation massive and produced into elongate rounded knob (size does not show clearly on Fig. 17 due to foreshortening), ventral articulation also massive and rounded, not elongated.

Prosthecal brush (Pr.) of long fine hairs. Small brush of shorter thicker hairs dorsad and caudad of prostheca. Campaniform sensillum (Cmp.) distal to dorsal articulation. Two large sensilla on aboral surface, the dorsal one spatulate (Ss.) with thin flared ends (Fig. 5, 6, 17).

Maxillae complex, massive, heavily sclerotized. Maxillary palp (Mxp.) one-segmented, at least 11 - 13 apical sensilla (Fig. 14) one showing distinct pores (Fig. 15). Sensilla surrounded by rosette of sclerotized projections, sometimes showing excessive wear (Fig. 16). Campaniform organ (Cmp.) proximal and aboral to rosette (Fig. 14, 16).

Distinct palpiger (Pp.) (Fig. 12). Stipes (St.) with two raised lobes one on either side of palpiger. Campaniform sensillum (Cmp.) directly below palpiger. Galea (Ga.) with series of teeth on distal edge, adoral sunken brush of hairs and sensilla, and adoral molar region, large basal lanceolate sensillum (ls.) (Fig. 13). Lacinia (La.) of one large lobe with two large curved sensilla (Fig. 12, 13). Cardo (Ca.) with one large curved sensillum and brush of hairs partly covered by hypostomal teeth (Hyp.) (Fig. 12).

Labrum membranous, with two lateral palatal brushes (Fig. 5, 9, 19) of curved hairs, pectinate distally (Fig. 11). Dorsad of each brush a group of at least five sensilla (Fig. 22). Dorsad and caudad of this group a single sensillum. Laterad of each brush an anteriorly directed cuticular projection (T.) (Fig. 5, 6) (Light microscopy shows muscles inserted at this region - it is probably part of the torma).

Messor (Ms.) (Fig. 10, 11) ventral and caudad of lateral palatal brushes on epipharyngeal surface (Ep.), consists of approximately 12 - 14 flattened curved spines, some distally serrated. Medial to each messor two cone-like epipharyngeal sensilla (Eps.) (Fig. 11).

Hypostomium a rectangular plate with curved edges and three-four blunt medial teeth. Expands caudad to articulate with broad gular sclerite (Fig. 19, 20). Labium not visible externally.

Body. Shape and length variable depending on treatment at time of death. Total body length (from behind head to tip of tracheal gills), $\overline{X} = 14.5 \pm 2.9$ mm; N = 23. Shape often semicylindrical, (Fig. 3) but mostly dorsoventrally flattened. In life, body shape highly variable. Body wall translucent in life, with rough, highly dissected, reticulate microsculpture and spatulate setae (Fig. 36).

Prothorax in two distinct regions (Fig. 25, 27). Spiracle located posteroventrally (Fig. 25). No ambulatory setae. Two pairs of podal hairs, (Pd. Fig. 27, 28; as in other thoracic segments these hairs mark the internal position of the imaginal leg histoblasts). Spiracle rounded and sunken into pit with central ecdysial scar (Ecds.) (Fig. 26). No apparent openings, but electron beam penetration indicates thin cuticle (preliminary examination of the internal structure shows the spiracles to be of Type II, Keilin 1944).

Mesothorax larger than prothoracic segment, not divided (Fig. 29). Two patches of ventral ambulatory setae (Amb.) and podal hairs (Pd.) (Fig. 29, 30).

Metathorax largest thoracic (and body) segment, as for mesothorax (Fig. 31). Ventral ambulatory setae (Amb.) and podal hairs (Pd.) (Fig. 32).

Abdomen of nine segments decreasing in size caudad, each with intercalary region, and each divided ventrally (Fig. 33) into two regions, no ambulatory setae (Fig. 34, 35). Segment 8 with two long filamentous tracheal gills (Trg.) (dissection and light microscopy shows only a trachea and a nerve in each filament) with spiracle (Sp.) at gill base (Fig. 37). Spiracle as for prothorax, but with minute pores showing clearly (Fig. 38). Segment 9 dorsal pair of filamentous tracheal gills (Trg.) (Fig. 3); four anal papillae (Anp.), two on each side of anus, showing polygonal cuticular patterning (Fig. 37); anus slit-like with large lips dorsoventrally; ventrally, two ambulatory pseudopods (Amp.), with tracheal gill arising before (Fig. 3) the distal rectractile portion of the pseudopod, which bears 18 - 23 slender, curved hooks directed ventrally (Dh.) and six - seven stouter hooks (Bh.) at their bases (Fig. 39).

BEHAVIOUR

Larval behaviour was observed in the laboratory under conditions quite different from those of the known habitat of the animal. Therefore, these observations should be interpreted with caution.

At rest, larvae are buried in the substrate with the filamentous terminal tracheal gills often protruding. Occasionally a small inverted cone-shaped pit is produced by the twisting of the filaments. The gills are held together in a loose bundle along with the pseudopods and anal papillae. When the gills are touched or the substrate disturbed the gills are retracted very rapidly. If the stimulus stops the gills are protruded again within a few minutes. If the stimulus is continued the larvae will start burrowing deeper into the substrate. When moving over the substrate the larva usually pulls itself forward with its head. The mandibles and labrum are retracted and the prognathous head is turned towards the substrate. The epistomal ridge is forced into the substrate and using this as a fulcrum the thorax is arched, thereby pulling the abdomen forward. As this happens the tracheal gills and pseudopods are actively held together forming a fine, streamlined tip to the abdomen. When the maximum forward movement of the thorax and abdomen has been achieved, the pseudopods and gills spread open and are pushed against the substrate or the pseudopod hooks grip any object available. This provides a posterior fulcrum for a forward thrust of the head and thorax. This series of movements is repeated.

For burrowing, larvae appear to need a point of resistance against which the dorsal thorax can press. An individual placed on fine sand has great difficulty burrowing, but if a small stone is present it uses this to force the thorax against, and thence the head into, the substrate. Once the head and thorax are buried the terminal gills and pseudopods are often held off the substrate and burrowing appears to be done only with the anterior part of the body. Observations of larvae in a substrate of clear glass beads showed that waves of contraction, causing the thorax to expand and contract, move forward along the body during burrowing. These contractions probably shift the substrate material, thereby allowing the thorax and head room for movement.

Larvae are strongly thigmotactic and when deprived of particulate substrate they thrash around strongly and rapidly until brought up against suitable material for normal movement.

Movement of Mouthparts

Definitive feeding behaviour of living larvae was not observed but the mouthparts move repetitively as the animal advances and plant material was constantly mouthed during such movements.

The mandibles are restricted to a lateral plane of movement, but could be protracted until the tips pointed directly forward. The membranous labrum with lateral palatal brushes filled the dorsal space between the mandibles, swelling and shrinking in perfect unison with the mandibular movements.

As the mandibles retract, their dorsal edges sweep the epipharyngeal region of the palatal brushes. The mandibular prosthecal brush sweeps the innermost epipharyngeal region of the palatal brushes. These prosthecal brushes are probably of considerable importance in feeding. At full mandibular protraction the prosthecal brushes cross the cibarium, and at full retraction the brushes must be directed down the cibarium and pharnyx. The lateral palatal and mandibular prosthecal brushes appear to collect and to push into the pharnyx plant material loosened by the mandibles.

The maxillae in action are difficult to see but appear to move in unison with the mandibles, though with far less lateral motion. There may be more involved than this for the sutures adjacent to the maxillae and hypostomium move a surprising amount, considering the head is so heavily sclerotized. Certainly the wear of the adoral surface and associated hairs of the galea (Fig. 13), and the wear of the maxillary palp tip (Fig. 16) indicates that the maxillae are used in grinding the food.

DISCUSSION

Of particular interest are the spectacular terminal tracheated appendages. Observations in the laboratory strongly indicate that these structures are gills. They were often kept above the gravel substrate while the rest of the animal's body was submerged, but could be rapidly retracted when the larva was disturbed.

Possession of long tracheal gills and apparently functional amphipneustic spiracles by third (?) instar larvae is interesting, because the second (?) instar larvae are only metapneustic with the spiracles apparently lacking openings. It is generally believed (Hennig 1973) that the holopneustic condition of Bibionidae larvae is basic to larval Diptera. However, Keilin (1944) and Hinton (1947) have shown that in larval Diptera the number of spiracles in early instars is always less than that of later instars. Hinton suggests respiratory requirements as the reason for this.

Larval *Eutanyderus wilsoni* from Australia lack spiracles, but one larva of an undescribed Australian tanyderid, supplied by H.B.N. Hynes, is amphipneustic. The implications of presence or absence of spiracles in tanyderid larvae will be discussed elsewhere at a later date.

Descriptions of larval *Protoplasa* and *Protanyderus* indicate antennae of three articles. However, the scanning electron microscope clearly shows pores in the distal structure (Fig. 15), indicating that the last "article" is a sensillum similar to that on the antennae of larval Simuliidae (Craig 1975). Therefore there are only two antennal articles. The antennae of the Australian *Eutanyderus wilsoni* larvae also have two articles and an apical sensillum (pers. obs.). Wood (1952) showed only one small antennal article with two distinct apical "papillae" in larval *Peringueyomyina barnardi,* but had difficulty in making observations on the very small antennae. Personal observations of *P. barnardi* larval antennae show two articles, the distal one very short, and at least three apical sensilla, one larger than the others.

The locomotor behaviour of larvae along the surface of the substrate is unusual. The head is heavily sclerotized, presumably to resist abrasion against the substrate, evidenced by heavy scratching of the cuticle on the epistomal ridge (Fig. 5, 22). The mandibles and maxillae are also worn, (Fig. 13, 16, 18) but it is not known if this is caused by the substrate or by hard food material.

Several morphological characteristics of tanyderid larvae are worthy of note in relation to their burrowing habit. The microsculpture of the body cuticle is very complex with no obvious reason, except to provide some protection against damage due to abrasion. Although the live cuticle is virtually transparent it is extremely tough. Likewise the tracheal gills appear delicate but are hard to damage. Broken gills plugged by black pigment were found in about half the larvae collected. In some instances the trachea would protrude through the pigment plug. The antennae are protected dorsally by a heavily sclerotized knob (Fig. 23), which also partly houses the dorsal articulation of the mandible.

Alexander (1930) commented on the lack of creeping welts on the ventral thorax and abdomen of *Protoplasa fitchii,* but Crampton (1930) describes ambulatory setae on the thorax. Although there are no distinct raised areas on the ventral thorax and abdomen of the Albertan tanyderid larvae, the scanning electron microscope shows distinct groupings of caudally directed setae on the thorax (Fig. 29-32). An ambulatory function seems clear for these setae.

That the head is heavily sclerotized anteriorly with protective devices for the antennae (Fig. 21, 23) and for the sensilla of the maxillary palp (Fig. 14), and that microsculpture and setae are in general directed caudad, indicate that larval tanyderids spend much time actively moving through the substrate. The filamentous tracheal gills and the cephalic hair sensilla are extremely tough, and the gills can be manipulated by the larvae to form a streamlined arrangement during burrowing. Indeed, the complete body appears to be well adapted to a burrowing life in gravel.

Alexander (1930) describes how he and Crampton initially began the search for *P. fitchii* larvae in logs submerged in the Pabos river, before finally searching in the gravel. As they suggested larvae eat vegetable material. Gut contents of three specimens, plus faecal material from live larvae, show only plant material similar to that found in the substrate. Certainly the mandibles are well adapted for handling fibrous, woody material. We think that one of the requirements for tanyderid habitats is the presence of ample organic remains in the substrate such as is found at Innisfail and the Old Man River sites. The only other information on feeding behaviour is for larval *Eutanyderus wilsoni* which live in and feed on the rotting surface of logs in Australian high alpine streams (Colless, *in litt.* 1975). Presumably the Alberta larvae feed on the detritus in the gravel substrate. Larvae kept in the laboratory were provided the detritus from the site from which they came, but showed few signs of feeding.

Tanyderidae are clearly widespread in Alberta and, although they are generally considered rare insects, this is probably due more to the arduous work involved in collecting them than to their paucity of numbers. The rarity also relates to our imperfect knowledge of their preferred habitat. Wood (1952) collected some 30 *Peringueyomyina barnardi* larvae easily from one locality, while the most we collected was seven in a day. Tanyderid larvae probably use the hyporheic zone for most of their life. Reports of tanyderid pupal habitats (Alexander 1930, Knight 1964, Wood 1952) suggest that the larvae migrate to the vicinity of banks and possibly pupate beyond the stream margins. These habitats are included in Schwoerbel's (1967) definition of the hyporheic zone.

Hyporheic habitats, where they occur, are associated with extensive gravel floodplains (Stanford & Gaufin 1974, Bishop, J.E. 1973) which are restricted to a particular reach of river between source and mouth. Upstream of these areas, rivers are characterized by steeper gradient and rubble type substrates, while downstream they tend to have fewer riffles and more silty substrate. Tanyderids were collected only in the middle reaches of the Old Man and Red Deer Rivers, even though collections of invertebrates were made further upstream and further downstream. However, substrates at other Alberta tanyderid locations indicate that larvae are not restricted to one type of habitat.

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ABBREVIATIONS

Amb.	Ambulatory setae	La.	Lacina
Amp.	Ambulatory pseudopod	Lb.	Labrum
Anp.	Anal papillae	Ls.	Lanceolate sensillum
Ant.	Antenna	Mnd.	Mandible
Aps.	Apical sensillum	Ms.	Messor
Bh.	Basal hooks	Mx.	Maxilla
Ca.	Cardo	Mxp.	Maxillary palp
Cmp.	Campaniform sensillum	Pb.	Lateral palatal brush
Dh.	Distal hooks	Pd.	Podal hairs
Ecds.	Ecdysial scar	Pp.	Palpifer
Ecs.	Ecdysial suture	Pr.	Prostheca
Ep.	Epipharynx	Sp.	Spiracle
Epr.	Epistomal ridge	Ss.	Spatulate sensillum
Eps.	Epipharnygeal sensilla	St.	Stipes
Ga.	Galea	T.	Torma (?)
Hyp.	Hypostomium	Trg.	Tracheal gill

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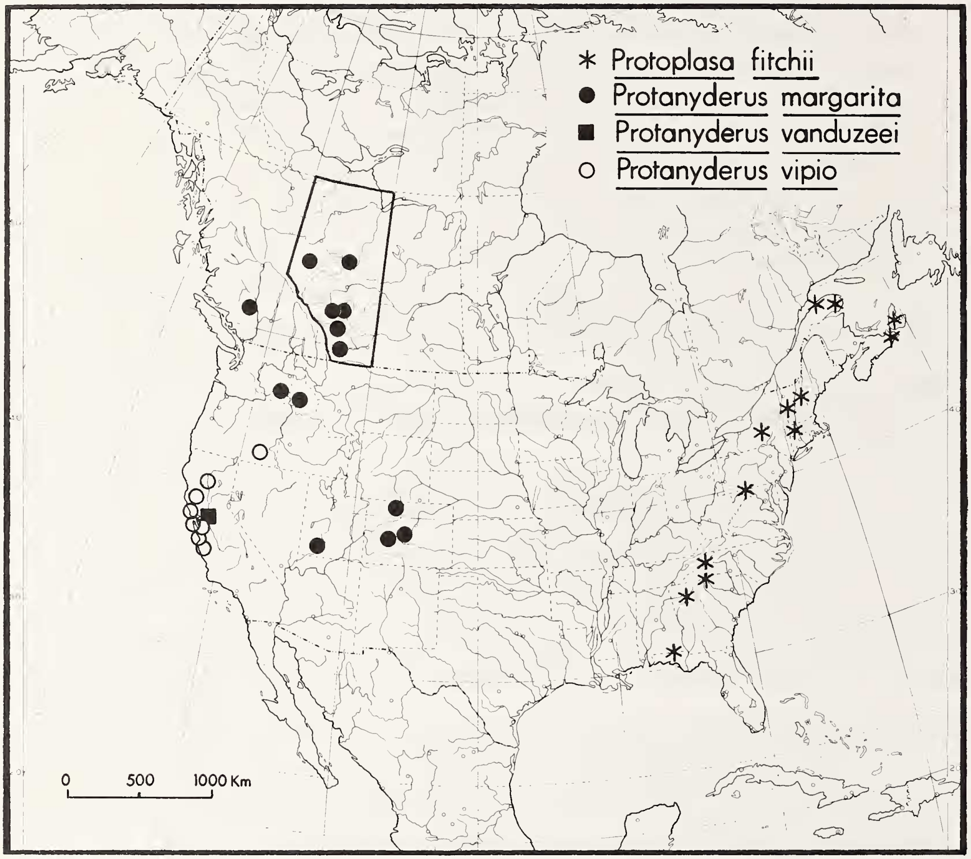
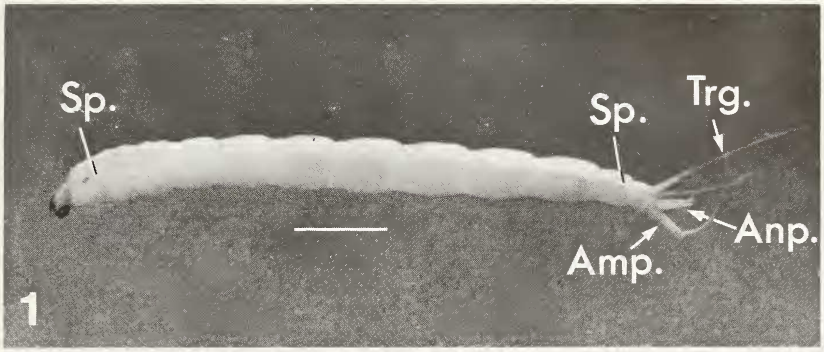


Map 1. General distributions of Tanyderidae in North America. Compiled from museum and literature records.



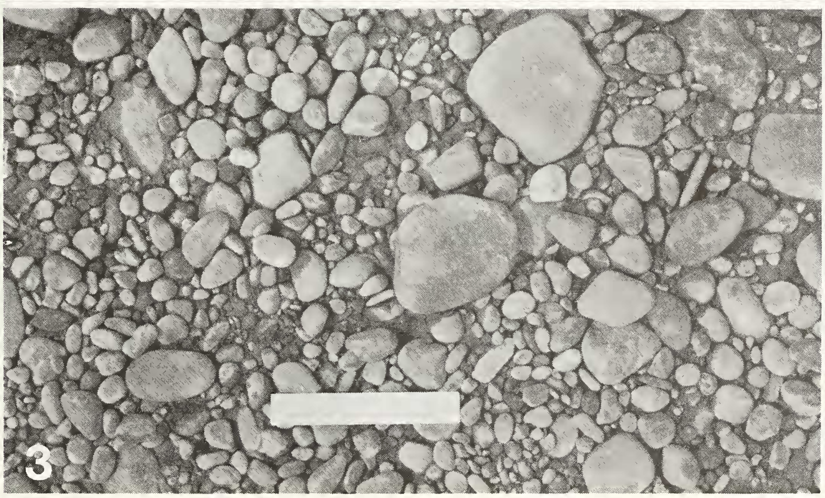


Fig. 1. Left lateral view of larval Tanyderidae from Sheep River, Turner Valley. Scale 2 mm. Fig. 2. Red Deer River flood plain, Innisfail site. Fig. 3. Innisfail site substrate. Scale 15 cm.

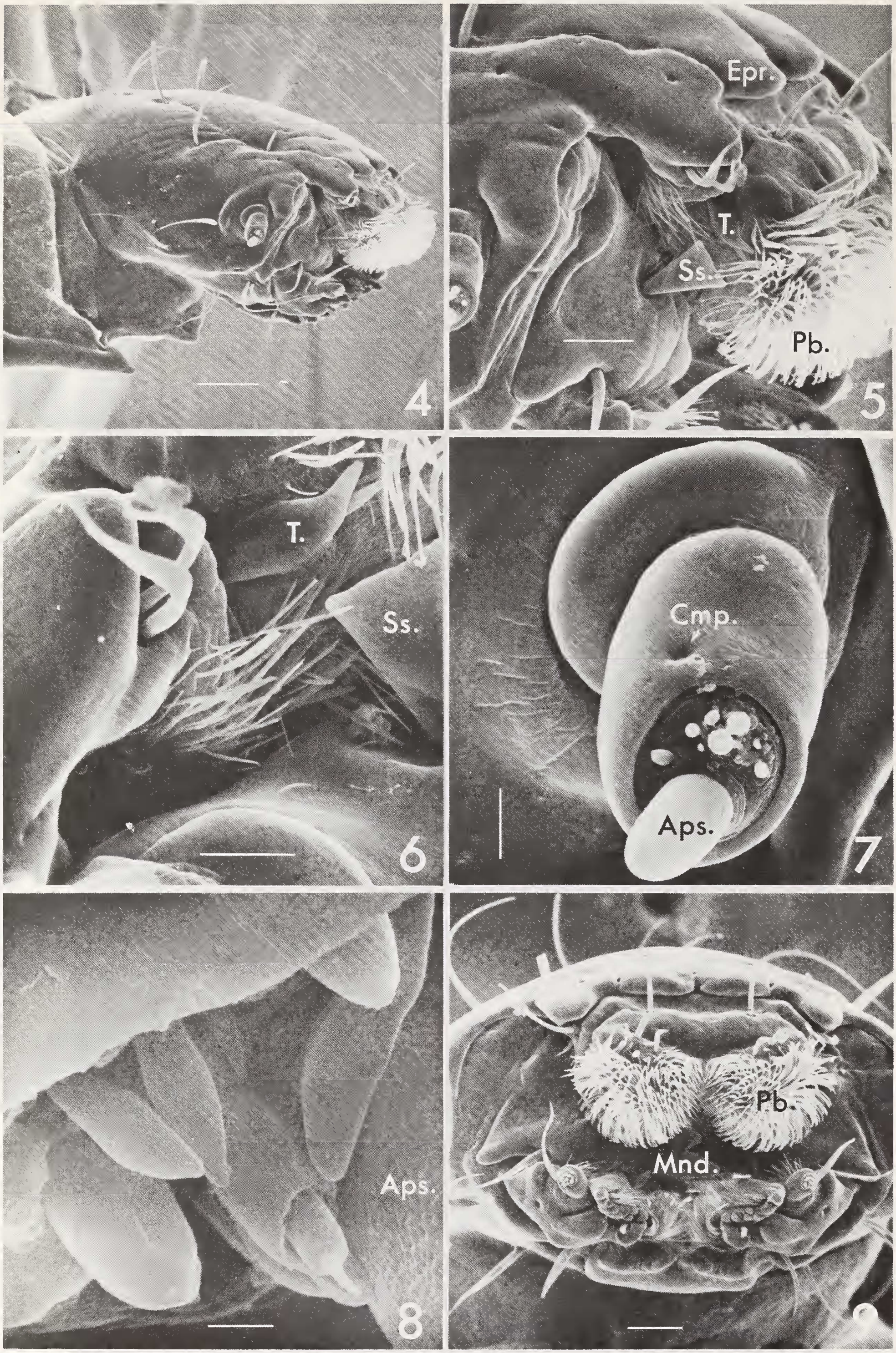


Fig. 4. Right lateral view of head. Scale 100 μm. Fig. 5. Head, right lateral view, higher magnification. Scale 50 μm. Fig. 6. Right antenna. Scale 20 μm. Fig. 7. Junction of right mandible, labrum and epistomal ridge. Scale 10 μm. Fig. 8. Antennal sensilla. Scale 50 μm. Fig. 9. Head, frontal view. Scale 50 μm.

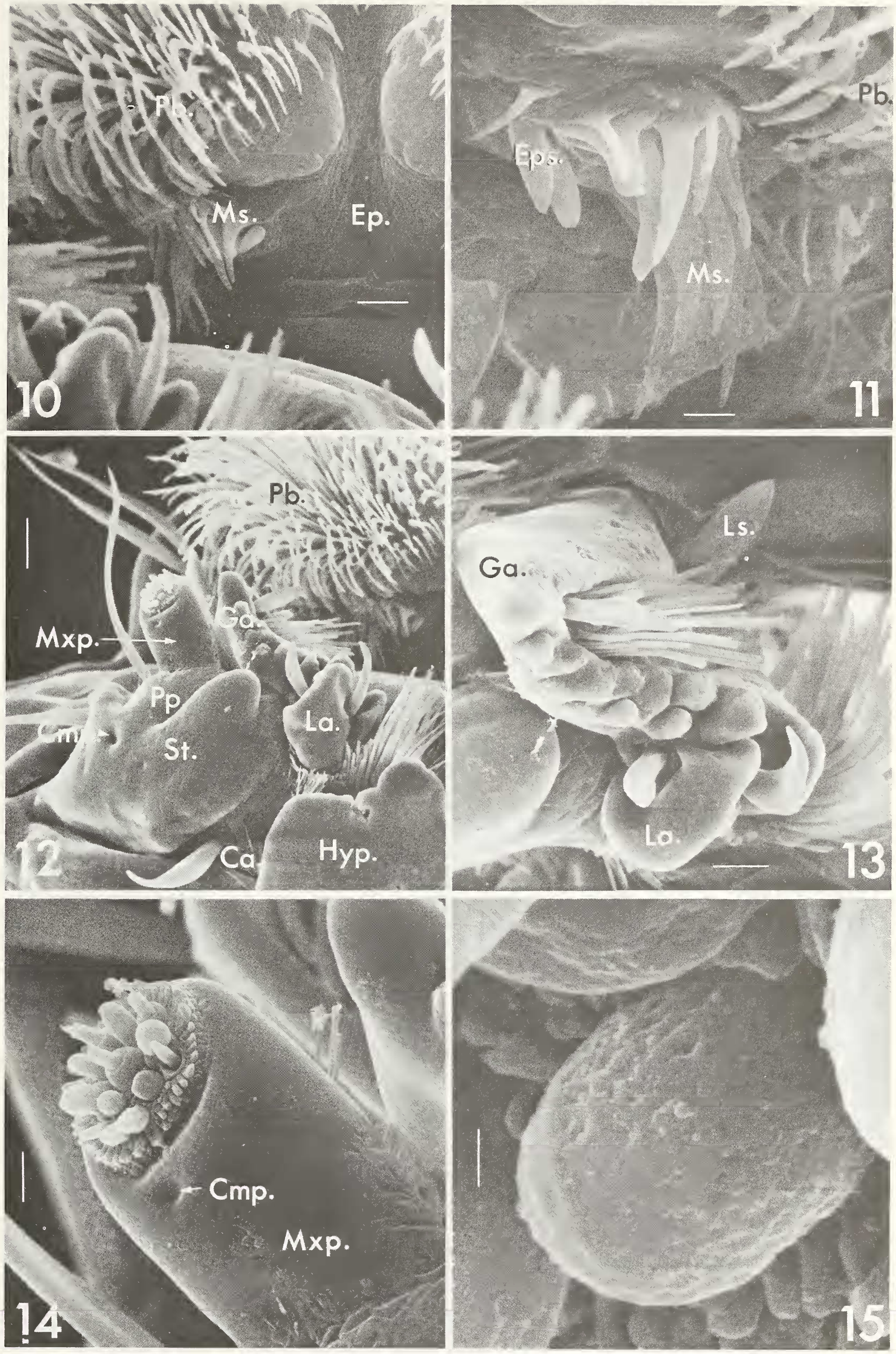


Fig. 10. Lateral palatal brushes and epipharynx, frontal view. Scale 10 µm. Fig. 11. Messor and epipharyngeal sensilla. Scale 5 µm. Fig. 12. Right maxilla, ventral view. Scale 20 µm. Fig. 13. Galea, adoral view. Scale 10 µm. Fig. 14. Apical sensilla, right maxillary palp. Scale 5 µm. Fig. 15. Pores in globular sensillum, maxillary palp apex. Scale 0.5 µm.

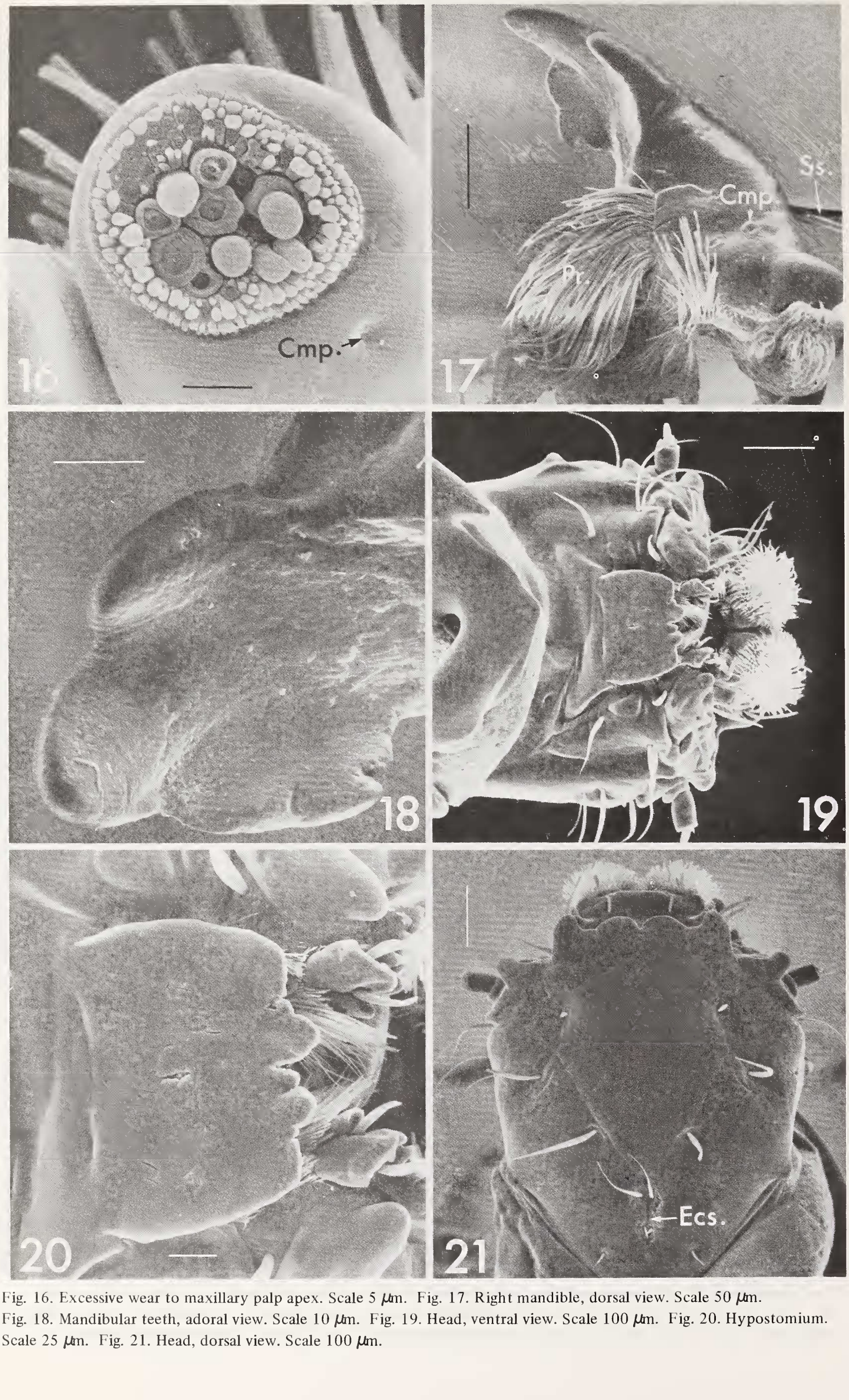


Fig. 16. Excessive wear to maxillary palp apex. Scale 5 μm. Fig. 17. Right mandible, dorsal view. Scale 50 μm. Fig. 18. Mandibular teeth, adoral view. Scale 10 μm. Fig. 19. Head, ventral view. Scale 100 μm. Fig. 20. Hypostomium. Scale 25 μm. Fig. 21. Head, dorsal view. Scale 100 μm.

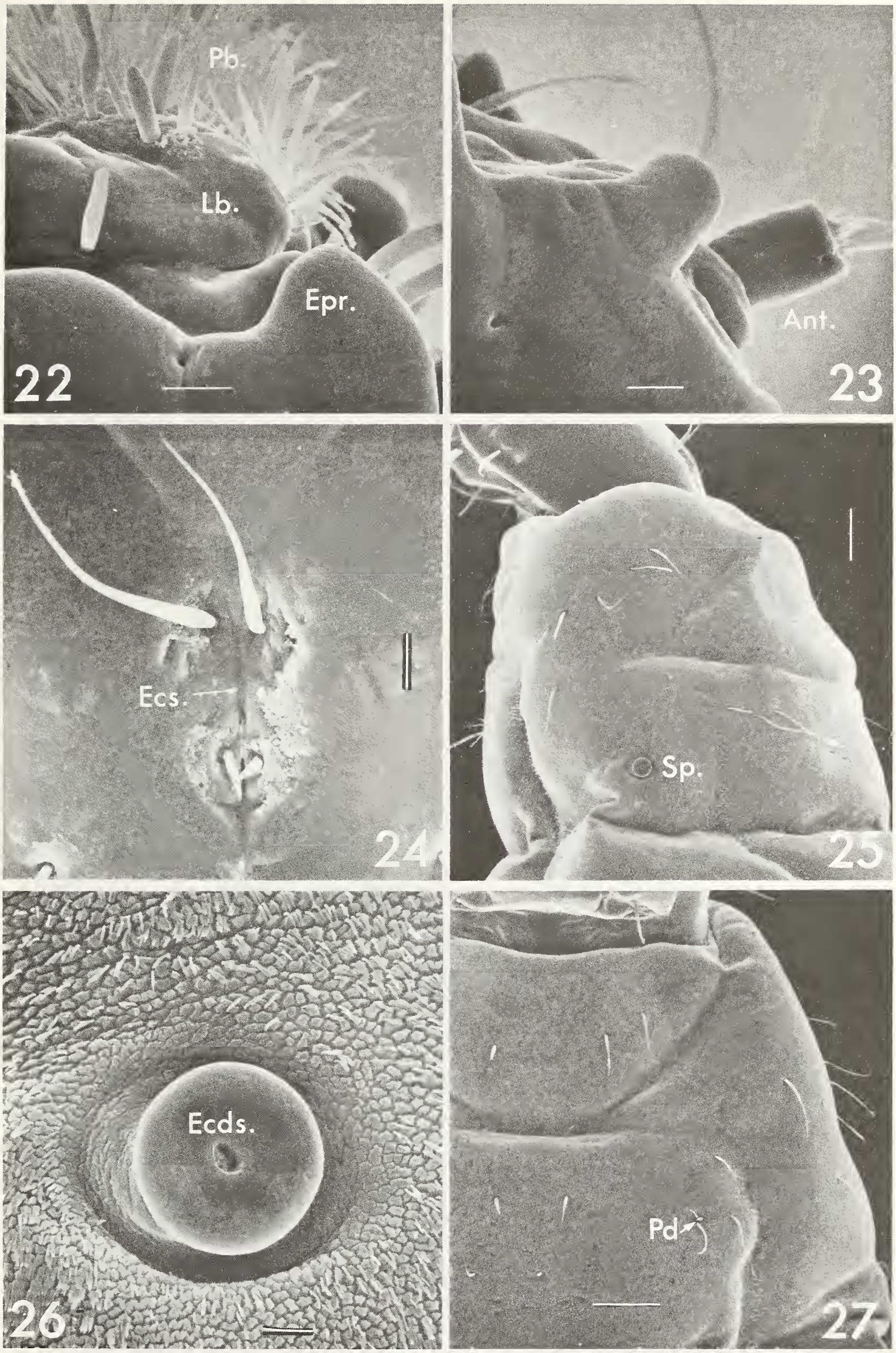


Fig. 22. Right lateral palatal brush and labral sensilla. Scale 20 μm. Fig. 23. Right antenna and protective knob. Scale 20 μm. Fig. 24. Ecdysial suture, showing invagination of cuticle. Scale 20 μm. Fig. 25. Prothorax and spiracle, left lateral view. Scale 100 μm. Fig. 26. Left prothoracic spiracle. Scale 10 μm. Fig. 27. Prothorax, ventral view. Scale 100 μm.

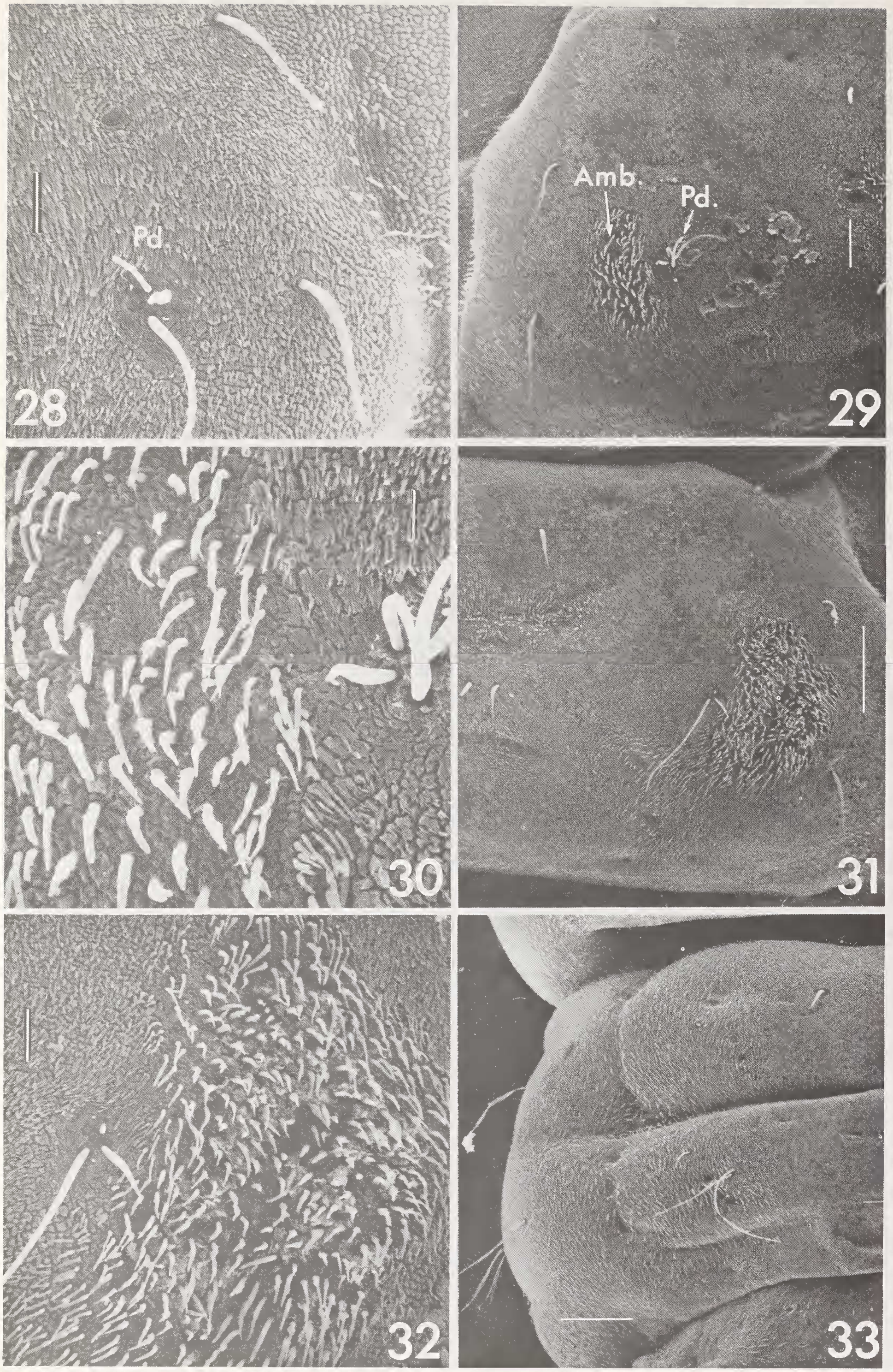


Fig. 28. Prothorax cuticular microsculpture, ventral view. Scale 20 μm. Fig. 29. Mesothorax, right ventral view. Scale 50 μm. Fig. 30. Mesothorax, ambulatory setae. Scale 10 μm. Fig. 31. Mesothorax, left ventral view. Scale 100 μm. Fig. 32. Metathorax, ambulatory setae. Scale 20 μm. Fig. 33. First abdominal segment, right ventral view. Scale 100 μm.

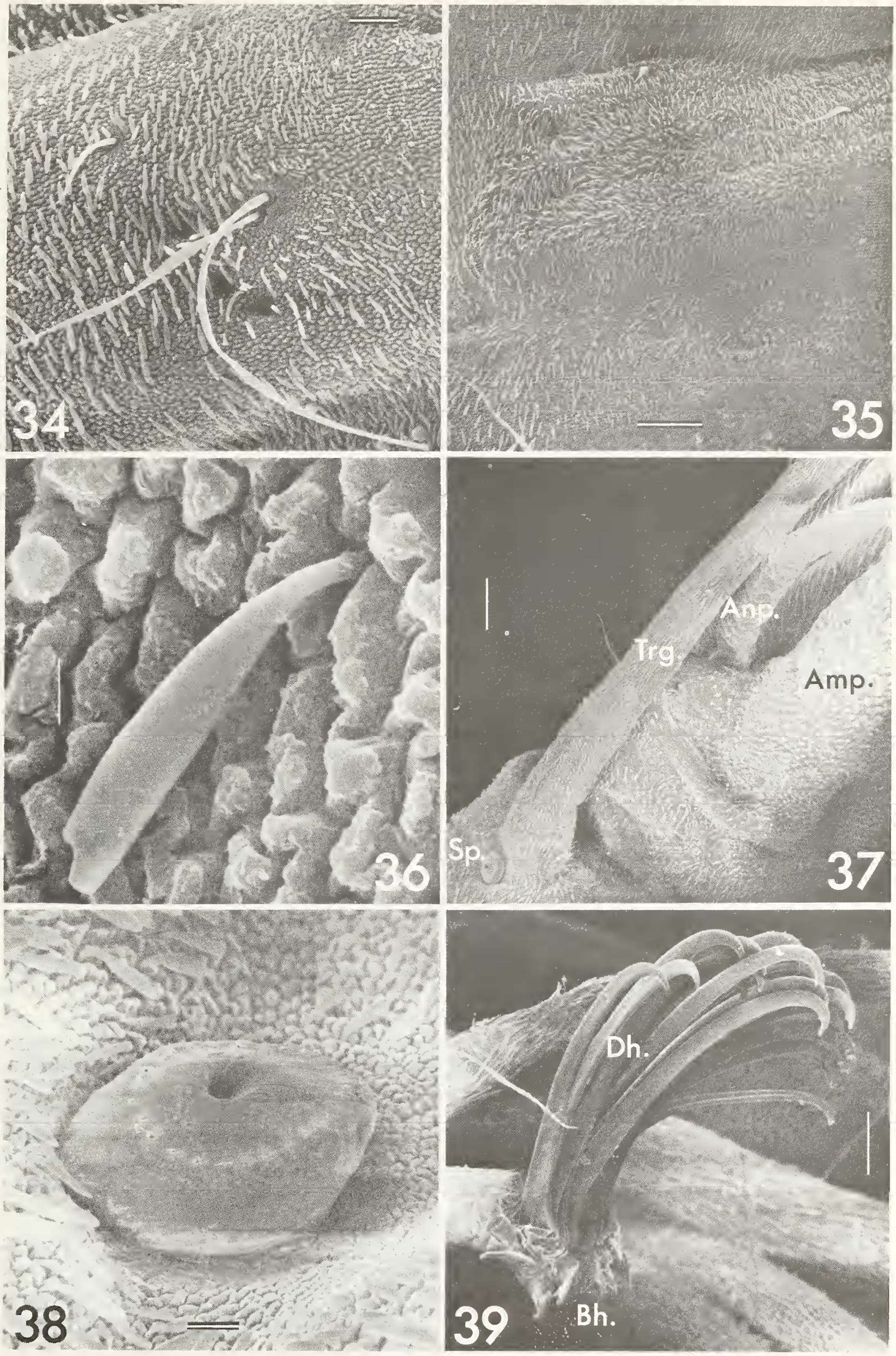


Fig. 34. First abdominal segment, setae and microsculpture. Scale 20 μm. Fig. 35. Second abdominal segment, right ventral view. Scale 50 μm. Fig. 36. Spatulate seta and microsculpture, abdominal segment. Scale 2 μm. Fig. 37. Bases of left pseudopod, anal papillae and tracheal gill. Note spiracle, Scale 100 μm. Fig. 38. Posterior abdominal spiracle, showing pores and ecdysial scar. Scale 10 μm. Fig. 39. Left abdominal pseudopod showing distal hooks. Scale 50 μm.